Proceedings of the Zoological Institute RAS
Vol. 320, No. 2, 2016, pp. 193–220

УДК 599.362 (597)

SECRETS OF THE UNDERGROUND VIETNAM: AN UNDERESTIMATED SPECIES DIVERSITY OF ASIAN MOLES (LIPOTYPHLA: TALPIDAE: *EUROSCAPTOR*)

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ABSTRACT

A study of the Southeast Asian moles of the genus *Euroscaptor* based on a combined approach, viz. DNA sequence data combined with a multivariate analysis of cranial characters, has revealed a high cryptic diversity of the group. An analysis of mitochondrial cytochrome *b* gene and five nuclear genes has revealed two deeply divergent clades: the western one (*E. klossi* + *E. malayana* + *E. longirostris* from Sichuan + *Euroscaptor* spp. from northern Vietnam and Yunnan, China), and the eastern one (*E. parvidens* s.l. + *E. subanura*). The pattern of genetic variation in the genus *Euroscaptor* discovered in the present study provides support for the existence of several cryptic lineages that could be treated as distinct species based on their genetic and morphological distinctness and geographical distribution. The moles from southern China and northern Vietnam form three distinct groups. The specimens from Sichuan (including the one collected from the type locality of *E. longirostris*) were clearly distinct from the northwestern Vietnam and Yunnan samples that were previously attributed to this species. We argue that the real distribution of *E. longirostris* is restricted to Sichuan, northward of Yangtze River, whereas the populations occurring southward of this isolation barrier evidently represent a new species *Euroscaptor orlovi* sp. nov. (northwestern Vietnam and Yunnan, southern China). Moreover, Red River that divides the western and eastern parts of northern Vietnam beyond doubt separates the population of *E. orlovi* from the moles occurring in northeastern Vietnam (Vinh Phuc and Cao Bang provinces); the latter are described here as *Euroscaptor kuznetsovi* sp. nov. Yet, genetic data are in favour of a close affinity of *E. subanura* with *E. parvidens*. A combined analysis of both genetic and morphological data has revealed a strong geographic segregation of *E. parvidens* samples. The populations from Dalat Plateau (southern Vietnam), including the moles from Loc Bao, Bi Dup and Chu Yang Sin, form a well-supported clade and can be considered true *E. parvidens*. The specimens from central Vietnam (Kon Tum and Quang Nam provinces) are significantly different from them, yet their monophyly has been supported by the mtDNA only. The moles from central Vietnam have been described here as a new subspecies *Euroscaptor parvidens ngoclinhensis* ssp. nov. All the studied samples of *E. subanura* have shown a low genetic and morphological variability despite their wide geographic range.

Key words: cryptic species, *Euroscaptor*, multilocus phylogeny, multivariate analyses, taxonomy

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ТАЙНЫ ПОДЗЕМНОГО ВЬЕТНАМА: НЕДООЦЕНЕННОЕ ВИДОВОЕ РАЗНООБРАЗИЕ АЗИАТСКИХ КРОТОВ (LIPOTYPHLA: TALPIDAE: *EUROSCAPTOR*)

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РЕЗЮМЕ

Исследование азиатских кротов рода *Euroscaptor* с применением комплексного подхода, включающего анализ ДНК и многомерный анализ краниологических признаков, выявило высокую криптическую изменчивость этой группы. Анализ митохондриального гена цитохрома *b* и пяти ядерных генов показал существование двух сильно дивергировавших клад: западная клада (*E. klossi* + *E. malayana* + *E. longirostris* из Сычуани + *Euroscaptor* spp. из северного Вьетнама и Юньнани, Китай) и восточная клада (*E. parvidens* s.l. + *E. subanura*). Картина генетической изменчивости рода *Euroscaptor*, выявленная в нашем исследовании, свидетельствует о существовании нескольких криптических линий, которые, на основании их генетических и морфологических различий и географического распространения, могут рассматриваться как отдельные виды. Кроты из южного Китая и северного Вьетнама образуют три отдельные группы. Экземпляры из Сычуани (включая экземпляр из типового местонахождения *E. longirostris*) заметно отличаются от кротов из северо-западного Вьетнама и Юньнани, которых ранее относили к этому виду. Мы считаем, что распространение *E. longirostris* ограничивается Сычуанью, к северу от р. Янцзы, тогда как популяции, обитающие к югу от этого изолирующего барьера, относятся к новому виду *Euroscaptor orlovi* sp. nov. (северо-западный Вьетнам и Юньнань, южный Китай). Река Красная, разделяющая западные и восточные районы северного Вьетнама, отделяет популяции *E. orlovi* от кротов, обитающих в северо-восточном Вьетнаме (провинции Виньфук и Каобанг), которые описаны здесь как новый вид *Euroscaptor kuznetsovi* sp. nov. Генетические данные свидетельствуют о близком родстве *E. subanura* и *E. parvidens*. Анализ генетических и морфологических данных выявил значительные географические различия между исследованными выборками *E. parvidens*. Популяции с Далатского плато (южный Вьетнам), включая кротов из Локбао, Бидупа и Чуянгсина, образуют отдельную кладу с хорошей поддержкой и могут рассматриваться как собственно *E. parvidens*. Экземпляры из центрального Вьетнама (провинции Контум и Куангнам) заметно отличаются от них, хотя монофилия этой группы поддержана только данными по митохондриальной ДНК. Кроты из центрального Вьетнама описаны здесь как новый подвид *Euroscaptor parvidens ngoclinhensis* ssp. nov. Исследованные выборки *E. subanura* характеризуются низкой генетической и морфологической изменчивостью, несмотря на широкое распространение.

Ключевые слова: криптические виды, *Euroscaptor*, мультилокусная филогения, многомерный анализ, таксономия

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INTRODUCTION

Asian moles of the genus *Euroscaptor* Miller, 1940 are widespread in the mountains and low hills of eastern and Southeast Asia. Hutterer (2005) recognized six species within *Euroscaptor*: *E. grandis*, *E. klossi*, *E. longirostris*, *E. micrura*, *E. parvidens* and *E. mizura*. Later, morphological and genetic data (Kawada et al. 2008) supported a species rank of the Malaysian mole *E. malayana*, which was previously included either in *E. micrura*, or in *E. klossi*. Recently, one more species, *E. subanura*, was described from Vietnam (Kawada et al. 2012). Despite the genus *Euroscaptor* has been addressed by a number of morphological and genetic studies (Motokawa 2004; Kawada 2005; Kawada et al. 2009, 2012; Zemlemerova et al. 2013; He et al. 2014; Shinohara et al. 2015), its species composition and limits remain controversial.

Molecular data by Shinohara et al. (2008) and Zemlemerova et al. (2013) indicated that the inclusion of the Japanese *E. mizura* in the genus *Euroscaptor* had definitely made it a paraphyletic taxon. Furthermore, Zemlemerova et al. (2013) argued that *E. mizura* belonged to a distinct phylogenetic lineage of a generic rank. Further studies have corroborated the occurrence of a deep split between *E. mizura* and the other Asian taxa of Talpini (He et al. 2014). Undoubtedly, this taxon has been awaiting its description as a separate genus (see also He et al. 2014 and Shinohara et al. 2014).

With the exception of *E. mizura*, seven species are now recognized in the genus *Euroscaptor* s.str., although the phylogenetic relationships among them remain disputable. The systematics and taxonomy of *Euroscaptor* species occurring in the Southeast Asia, especially in Vietnam, have not been sufficiently resolved yet. Vietnam bears one of the most diverse fauna of fossorial moles in Southeast Asia. There are at least five species of Talpidae including three species of *Euroscaptor*: *E. longirostris*, *E. parvidens* and *E. subanura* (Kawada et al. 2012; Abramov et al. 2013a). Previous genetic studies of *Euroscaptor* in Southeast Asia, including Vietnam (Zemlemerova et al. 2013; He et al. 2014; Shinohara et al. 2014), revealed a remarkable intraspecific variation that is indicative of cryptic regional species diversity.

In the present paper, we have undertaken a multilocus analysis of the phylogenetic relationships within *Euroscaptor* from Southeast Asia, with a special focus on the issues that remain controversial, such as phylogenetic positions of the taxa from Vietnam. A multivariate analysis of cranial characters has been used to estimate a morphological variation among the Vietnamese populations. Essential changes to the *Euroscaptor* taxonomy are presented below.

MATERIALS AND METHODS

Taxon sampling

The original material for the molecular phylogenetic study consists of 36 specimens of three currently recognized *Euroscaptor* species, 12 specimens of *Mogera* and *Talpa* and 16 specimens of four other Talpidae genera (*Desmana*, *Galemys*, *Parascalops*, *Condylura*). All the studied *Euroscaptor* specimens were collected in 2004–2015 from the 10 localities across Vietnam (Fig. 1) during the biodiversity surveys carried out by the Joint Vietnam-Russian Tropical Research and Technological Centre. Voucher specimens are deposited in the Zoological Institute of the Russian Academy of Sciences (ZIN, Saint Petersburg) and Zoological Museum of Lomonosov Moscow State University (ZMMU, Moscow). A list of the analysed specimens, including their collection localities and museum catalogue numbers, is provided in Table 1.

Additional 87 sequences of *Euroscaptor*, 10 sequences of *Mogera*, 20 sequences of *Talpa*, 5 sequences of *Scaptochirus*, 18 sequences of *Parascaptor* and 18 sequences of *Desmana moschata*, *Galemys pyrenaicus*, *Parascalops breweri* and *Condylura cristata* were downloaded from GenBank (Appendix 1) and used in the phylogenetic analyses.

DNA extraction, PCR amplification and sequencing

Pieces of muscle fixed in 96% ethanol were used as the sources for DNA extraction. Standard protocols for the genomic DNA extraction from ethanol-preserved tissues was employed, following proteinase K digestion, phenol-chloroform deproteinisation and isopropanol precipitation (Sambrook et al. 1989). We have sequenced the complete mitochondrial cytochrome *b* (*cytb*) gene and fragments of five nuclear loci: exon 11 of the breast cancer type 1 susceptibility protein (*BRCA1*), breast cancer type 2 susceptibility protein (*BRCA2*), apolipoprotein B (*ApoB*), recombination activating gene 1 (*RAG1*) and α-2b adren-



Fig. 1. Map showing the collecting localities of the studied specimens. The specimens collected during the present study are indicated by circles, the specimens from GenBank are indicated by squares. Locality codes see in Table 1 and Appendix 1. The type localities for *Euroscaptor* spp. are indicated by stars.

Table 1. List of the original material for *Euroscaptor* used for genetic and morphological analysis: species name, ID of specimens, collection and geographic location. The samples were retrieved from the following museum collections: ZMMU – Zoological Museum of Moscow State University, Russia; ZIN – Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia, BMNH – Natural History Museum, London, UK.

Species	Specimen code in phylogenetic trees (Figs. 2–3 ref.)	Museum catalog number where it is available	Collecting locality and locality code (Fig. 1 ref.)
Euroscaptor parvidens	Eupar 33	ZIN 96663	Vietnam, Kon Tum Province, Dac Glei District, 2–3 km west of Ngoc Linh Mt., 15°05´N, 107°57´E (6)
	Eupar 84	ZIN 96664	
	Eupar 85	ZIN 96665	
	Eupar AVA 14-038	ZIN 101920	Vietnam, Dak Lak Province, Krong Bong District, Chu Yang Sin National Park, 12°25´26´´N, 108°21´52´´E (7)
	Eupar AVA 14-041	ZIN 101921	
	Eupar AVA 14-074	ZIN 101922	
	Eupar AVA 14-075	ZIN 101923	
	Eupar AVA 14-037	ZIN 102246	
	Eupar AVA 14-082	ZIN 102247	
	Eupar 12	ZIN 98916	Vietnam, Lam Dong Province, Lac Duong District, 5 km NE of Long Lanh Village, Bi Dup – Nui Ba Nature Reserve, 12°10´44´´N, 108°40´44´´E (8)
	Eupar 15	ZIN 98917	
	Eupar 16	ZIN 98918	
	Eupar 17	ZIN 98919	
		ZMMU S-173400	
	Eupar 09.04.13-2	ZMMU S-195070	Vietnam, Lam Dong Province, Bao Lam District, Loc Bao Forestry, 11°44.304´N, 107°42.140´E (9)
	Eupar 09.04.13-1	ZIN 101901	
	Eupar 15.04.13-2	ZMMU S-195071	
	Eupar 14.04.13-1	ZIN 101902	
Euroscaptor sp.1	Eu 18	ZIN 96318	Vietnam, Lao Cai Province, 6 km west of Sa Pa, north slope of Fansipan Mt., near Tram Ton forest station, 22°21´N, 103°46´E (1)
	Eu 146	ZIN 98142	
	Eu 167	ZIN 97789	
		ZIN 101559	
		BMNH 33.4.1.148	Vietnam, Lao Cai Province, Sa Pa (1)
	Eu 99335	ZIN 99335	China, Yunnan Province, Jingdong County (10)
Euroscaptor sp.2	Eu AVA 12-288	ZIN 101531	Vietnam, Vinh Phuc Province, vicinity of Tam Dao, 21°27´06´´N, 105°38´09´´E (2)
	Eu AVA 12-289	ZIN 101532	
		ZMMU S-161162	
Euroscaptor longirostris		ZIN 6354	China, Sichuan Province, Chodsigou Valley (north of Lunganfu Town), 32°21´N, 104°20´E (11)
		ZIN 6374	
		ZIN 6373	
		BMNH 55.429	China, Sichuan Province, Tsao-Po
		BMNH 55.430	
		BMNH 55.431	
		BMNH 55.433	
		BMNH 55.435	
		BMNH 11.2.1.24	China, Sichuan Province, Omi-San (12)
		BMNH 99.3.1.9	China, Sichuan Province, Yangliupa
Euroscaptor subanura	Eusub AVA 12-276		Vietnam, Tuyen Quang Province, Son Duong District, Hiep Hoa Commune, 3 km east of Vuoc Ly Village, (northwestern slope of Tam Dao Mountain), 21°38´08´´N, 105°27´35´´E (3)
	Eusub AVA 12-277	ZIN 101533	
	Eusub AVA 12-278	ZIN 101534	
		ZIN 101535	
	Eusub AVA 13-030	ZIN 101897	Vietnam, Ba Vi District, 50 km west of Hanoi, vicinity of Ba Vi Resort, 21°04´58´´N, 105°22´54´´E (5)
	Eusub AVA 13-033	ZIN 101898	
	Eusub AVA 13-036	ZIN 101899	
	Eusub AVA 13-037	ZIN 101900	
	Eusub AVA 14-098	ZIN 101924	Vietnam, Phu Tho Province, Thanh Son District, Xuan Son National Park, 21°08´11´´N, 104°56´11´´E (4)
	Eusub AVA 14-103	ZIN 101925	
	Eusub AVA 14-104	ZIN 101926	
	Eusub AVA 14-108	ZIN 102248	
	Eusub AVA 14-115	ZIN 101927	
	Eusub AVA 14-117		
		ZIN 102249	
		ZIN 102252	
		ZIN 102254	
		ZIN 102255	

ergic receptor (*A2ab*). The primers for amplification and sequencing have been retrieved from different publications (Teeling et al. 2000; Ohdachi et al. 2001; Sato et al. 2004; Shinohara et al. 2004; Lebedev et al. 2007; Kirihara et al. 2013; Bannikova et al. 2015). The internal primers for *A2ab* sequencing have been designed specifically for this study: L540a 5`-ccttgtctacctgcgcatctatctg-3` and R930 5`-gggctacaagcygaggcaggaga-3`.

The PCR protocol for all genes has been as follows: initial denaturation at 94°C for 3 min, then 30 cycles of 94°C for 30 s, 52–65°C (depending on the primer pair) for 1 min, and 72°C for 1 min, with a final extension of 72°C for 6 min. PCR products were visualised on 1.5% agarose gel and then purified using ammonium ethanol precipitation. Approximately 10–30 ng of the purified PCR product have been used for sequencing with each primer by the autosequencing system ABI 3100-Avant using the ABIPRISMRBigDyeTM Terminator v. 3.1 (Applied Biosystems, Foster City, CA, USA).The sequences obtained in this study can be accessed via GenBank (Accession numbers see in Appendix 2).

Phylogenetic analysis

Alignment, partitioning and base composition

All sequences have been aligned by eye using Bioedit version 7.0.9.0 (Hall 1999). Heterozygous positions (at which two peaks of approximately equal intensity are observed) have been coded using the IUB ambiguity codes. In all analyses, sequences were used as unphased genotypes. Phylogenetic reconstructions have been performed with the following data sets: (1) an extended sample of taxa for *cytb*; (2) each nuclear gene separately; (2) all nuclear genes combined; (4) nuclear and mitochondrial *cytb* sequences combined in a species-tree estimation.

We have determined the best partitioning strategy for nuclear concatenation using the program Partition Finder (Lanfear et al. 2012) and developed five a priori candidate schemes: (1) partitioning by gene; (2) partitioning by codon position; 3) partitioning by gene and codon position (three subsets per gene); (4) as in variant 3 but with the 1st and 2nd codon positions combined (2 subsets per gene) and (5) no partitioning. The *cytb* data set has always been partitioned into three codon positions.

Pairwise genetic distances of the *cytb* gene sequences have been estimated using the Kimura-2 parameter model (Kimura 1980) implemented in MEGA5 (Tamura et al. 2007).

Phylogenetic tree reconstruction and species delimitation

Phylogenetic trees have been generated by maximum likelihood (ML), Bayesian inference (BI) and maximum parsimony (MP). An unweighted parsimony analysis has been performed in PAUP*4.0b10 (Swofford 2003).The following options were invoked: random addition sequence with 20 replicates, no limit for the number of optimal trees and TBR–branch swapping. Clade stability has been assessed based on 1000 bootstrap replicates obtained with the same tree search parameters.

ML analysis has been performed in Treefinder (October 2008 version) (Jobb 2008). To reconstruct the ML tree, appropriate models of sequence evolution selected for each partition, employing the routine implemented in Treefinder and using BIC as the criterion. Separate model has been determined for each of the three codon positions. The following options have been used in a tree search: parameter optimisation simultaneous with tree search, optimised partition rates, proportional branch lengths for all partitions, and maximum search depth. Bootstrap analysis (1000 pseudoreplicates) has been performed with model parameters and partition rates fixed at the values optimal for the ML topology.

The Bayesian analysis has been conducted using MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). Models with either two or six rate matrix parameters were selected for each partition based on the results of the model selection in Treefinder. Each analysis included two independent runs of four chains (one cold plus three heated following the default settings). The chain length was set at 20 million generations with sampling every 5000 generations. With these settings, the effective sample size exceeded 200 for all estimated parameters. Tracer 1.5 software (Rambaut and Drummond 2005) has been used to check for convergence and determine the necessary burn-in fraction, which was set to 2 million generations in all cases.

To construct the species tree from data on six potentially discordant independent loci (including *cytb*), we have employed a Bayesian coalescent framework as implemented in *BEAST (Heled and Drummond 2012). The units of the analyses correspond to species or well-supported groups as inferred

in the Automatic Barcode Gap Discovery (ABGD) analysis (Puillandre et al. 2012) of the *cytb* alignment. The automatic identification of the "barcode gap" has been performed using the ABGD application available at http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html under the following parameters: Prior minimal distance 0.01, Prior maximal distance 0.1 and relative gap width 1.0. A matrix of pairwise K2P distances was taken as input.

The molecular clock assumption has been tested separately for each gene using likelihood ratio tests with likelihood values calculated in PAML 4.7 (Yang 2007). Following the results of the molecular clock tests, we have used separate strict clock models for nuclear genes except *BRCA1* and an uncorrelated lognormal relaxed clock model for the mtDNA and *BRCA1*. No calibration information was utilised, and the mean rate for *A2ab* was set to one. We have used the same partitioning scheme and models as in the ML analysis. Yule prior for the species tree shape and the piecewise constant population size model were assumed. Default priors were used for all other parameters. In total, we have conducted four runs of 500 million generations each in BEAST version 1.8.0 (Drummond et al. 2012). Parameter convergence has been assessed in Tracer 1.5.

To validate potential species boundaries, we analysed the relationships between cryptic lineages in *E. longirostris* group using a multilocus species delimitation method, implemented in the BPP 2.1 software (Rannala and Yang 2003; Yang and Rannala 2010). The analysis was performed based on the combination of one mitochondrial and five nuclear loci. We used Gamma (2,100) as a prior distribution for both θ and τ. The relative rates of the loci were fixed at values inferred by *BEAST. The MCMC parameters were as follows: chain length of five million generations, burn-in period of ten thousand generations, and sampling frequency set at 1/1000.

Morphological analysis

Eighteen cranial variables have been measured following Kawada et al. (2007) using a digital caliper with an accuracy of 0.01 mm: greatest length of the skull (GLS), condylobasal length (CBL), palatal length from the anterior tip of the 1st incisor to the posterior lip of the palate (PL), inner length of the zygomatic arch (LZA), length of the upper tooth row (I1–M3), distance between the upper canine and 3rd molar (C–M3), length of the upper molars (M1–M3), rostral breadth of the canines (RB), breadth between the infraorbital foramina (BIOF), breadth across the upper 2nd molars (BAM), greatest interorbital breadth (IOB), braincase width (BCW), braincase height (BH), mandible length (MdL), mandible height at the coronoid process (MH), length of the lower toothrow (i1–m3), distance between the lower 1st premolar and 3rd molar (p1–m3), length of the lower molars (m1–m3). In total, 47 skulls from the collections of ZIN, ZMMU and the Natural History Museum (BMNH, London) have been examined. External measurements available on museum tags, apparently representing the measurements obtained in the field by original collectors, have been used for comparison.

The principal components analysis (PCA) and the canonical discriminant function analysis (DFA) have been used to evaluate a degree of cranial differentiation. The software program Statistica 8.0 (StatSoft Inc., Tulsa, OK, USA) has been used for all analytical procedures. Males and females were combined in the analysis, because the sexual dimorphism was earlier reported to be insignificant (Abe 1967; Kawada et al. 2012).

RESULTS

Alignment and partitioning in the DNA analysis

In the combined analyses of five nuclear genes, the final alignment consists of 4890 nucleotide positions including 1206 bp of *BRCA1*, 951 bp of *ApoB*, 816 bp of *BRCA2*, 1011 bp of *RAG1* and 906 bp of *A2ab*. On the whole, the data set contains 71 specimens including 4 outgroups. The final alignment of *cytb* includes 1140 bp for 81 specimens including 4 outgroups. The optimum partitioning scheme for the nuclear genes identified by Partition Finder under the BIC criterion corresponds to the variant 4 (partitioning by the gene and codon position but with the 1st and 2nd positions combined). The best-fit substitution models employed for each of the subsets are given in Appendix 3.

Phylogenetic analysis of the cytb data

On the Fig. 2 the ML tree is shown with the values above the branches that correspond to the Bayesian posterior probabilities in BI and the bootstrap

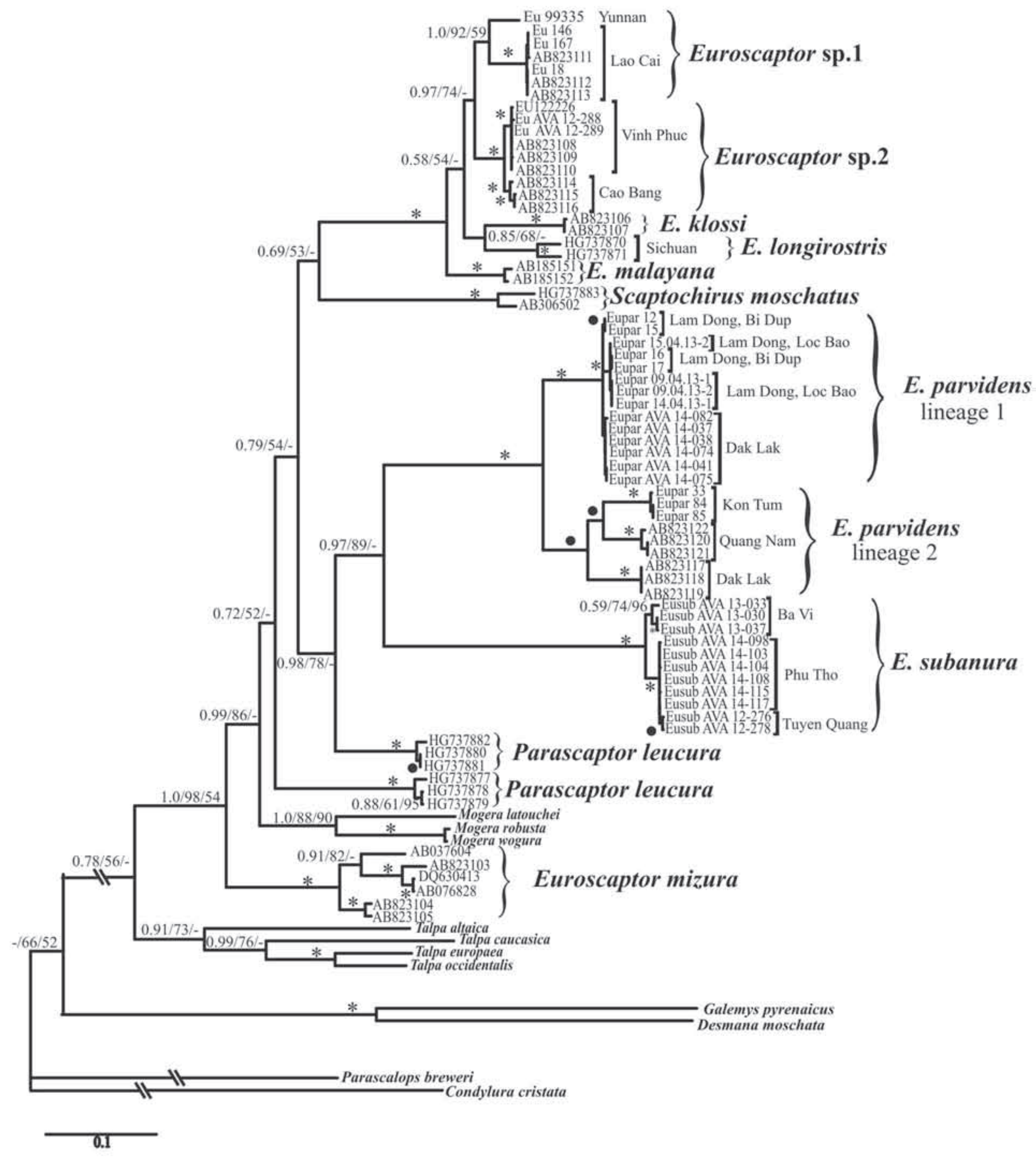


Fig. 2. The ML phylogeny of the genus *Euroscaptor* as inferred from the complete *cytb* gene sequence. Values above the branches correspond to Bayesian posterior probabilities in MrBayes (BI) and bootstrap support (1000 pseudoreplicates) in ML and MP analyses, correspondingly. The asterisks denote the highly supported nodes in all analyses (Bayesian posterior probabilities BPP >0.95, ML and MP bootstrap support >90%); filled circles mark moderately supported nodes (Bayesian posterior probabilities (BPP)>0.85, ML>70%). Representatives of the genera from the tribes Desmanini, Scalopini and Condylurini are used as outgroups.

support in ML and MP analyses. This mitochondrial phylogenetic tree has not supported the monophyly of the genus *Euroscaptor*, since the Japanese species *E. mizura* was recovered as the basal branch for all the Asian fossorial moles, while the branches of *Scaptochirus* and one of the *Parascaptor* species appeared within the radiation of *Euroscaptor*.

With the exception of *E. mizura*, all the *Euroscaptor* species are subdivided into two clades. All the analyses (BI, ML and MP) have strictly supported a clade comprising *E. klossi, E. malayana, E. longirostris* from Mouping (China, Sichuan), which is the type locality of this species, and an unknown form – *Euroscaptor* sp. – from northern Vietnam and southern China (Yunnan). *Scaptochirus moschatus* shows a tendency to join with this clade, however the support of this association is low (MI, ML) or absent (MP). The genetic distance (K2P) between *E. longirostris* from Sichuan and *Euroscaptor* sp. from northern Vietnam and Yunnan is about 8%. *Euroscaptor* sp. is also subdivided into two subgroups: north-west one (*Euroscaptor* sp.1) and north-east one (*Euroscaptor* sp.2), with the genetic distance between them being 6%. Within each of these subgroups, additional haplogroups have been found; each corresponds to the specific geographic localities: Yunnan and Lao Cai within the first lineage, Vinh Phuc and Cao Bang – within the second one.

The second clade of *Euroscaptor* includes *E. parvidens* s.l. and *E. subanura*, forming a sister group to that of the *Parascaptor leucura* branch, with the moderate BI and ML. The sister relationships *E. parvidens* s.l. with *E. subanura* shows a high support (K2P-distance between them ~ 17%). The grouping *E. parvidens* s.l. turns out to be heterogeneous: all geographic samples form distinct clades with K2P-distance between them from 6.1% to 9.5%, which in turn form two main subgroups: southern and central ones. The first one is geographically close to the type locality and includes the specimens from Dalat Plateau (Loc Bao, Bi Dup and Dak Lak); the second one originates from the Central Highlands, or Kon Tum Plateau (the specimens from Kon Tum, Quang Nam and few GenBank samples labeled as “Dak Lak”, see Table 1 and Appendix 1). Thus, the specimens from Dak Lak have been allocated into two different subgroups: our own sequences belong with the southern clade, whereas the sequences from GenBank group with the central clade. In the following text, we have named these two clades as the *E. parvidens* lineage 1 (southern Vietnam) and the *E. parvidens* lineage 2 (central Vietnam: Kon Tum and Quang Nam).

Species delimitation using ABGD and BPP

For purposes of species delimitation, the ABGD method has been applied to our *cytb* data set (Puillandre et al. 2012), which seems functional in the absence of reliable *a priori* taxonomic information. Based on the frequency distribution of K2P values between *cytb* haplotypes, the ABGD has retrieved 14 groups for primary partitions. The 14 group solution corresponds to the following partition: the *E. parvidens* lineage 1, three groups within the *E. parvidens* lineage 2, two groups within *Euroscaptor* sp.1, *Euroscaptor* sp.2, *E. longirostris*, *E. subanura*, *E. malayana*, *E. klossi* and three groups within *E. mizura*. In general, these groups correspond to the main clades on the phylogenetic *cytb* tree (Fig. 2).

The multilocus BPP analysis provided strong support (posterior probability is 1.00) for the recognition of *Euroscaptor* sp.1 and *Euroscaptor* sp.2 as separate lineages.

Phylogenetic analysis of the nuclear data set

The results of combined analysis, as well as those obtained on the basis of each independent gene, are presented in Figs 3 and 4. Neither of the alternative relationships obtained from individual gene trees has received strong support; therefore, we have analysed the concatenated sequence of five genes. Based on the nuclear concatenation, all methods have reconstructed identical trees with the strong support for most of nodes. On the Fig. 3 only the ML tree with the bootstrap support values for the ML and MP and the posterior probabilities of the Bayesian analysis on each node is shown.

On the ML-tree inferred from a concatenated alignment of five nuclear genes (Fig. 3), the genus *Euroscaptor* (with the exception of *E. mizura*) is monophyletic in relation to *Scaptochirus moschatus* and *Parascaptor*, which are also monophyletic. Just as the case of *cytb,* two clades are strongly supported within *Euroscaptor* s.str.: (1) *E. klossi*+*E. malayana*+*E. longirostris* from Mouping + *Euroscaptor* spp. from northern Vietnam and southern China (Yunnan); (2) *E. parvidens* s.l. +*E. subanura*. How-

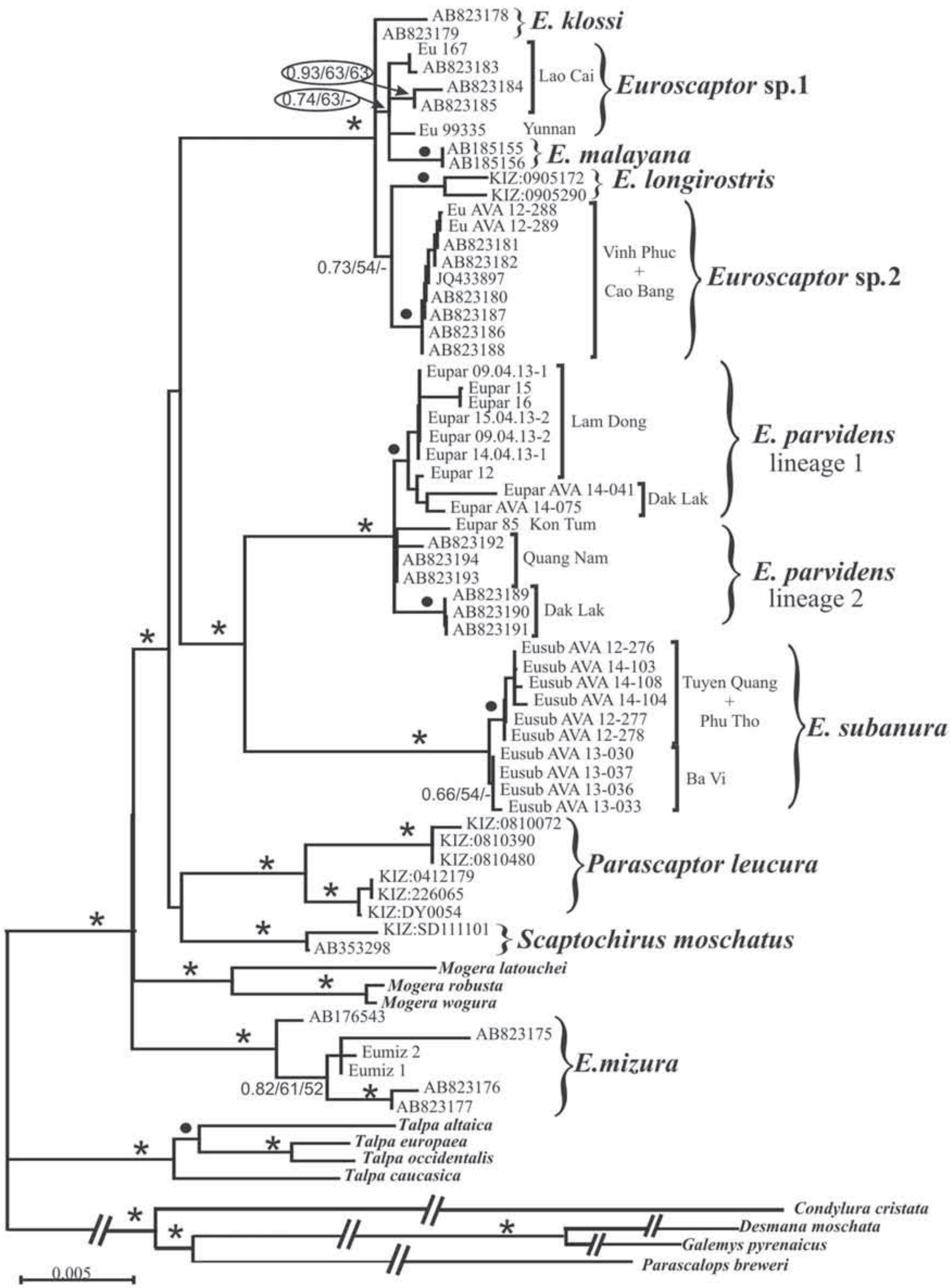


Fig. 3. The ML phylogeny of the genus *Euroscaptor* as inferred from a concatenated alignment of five nuclear genes. The designations are as in Fig. 2.

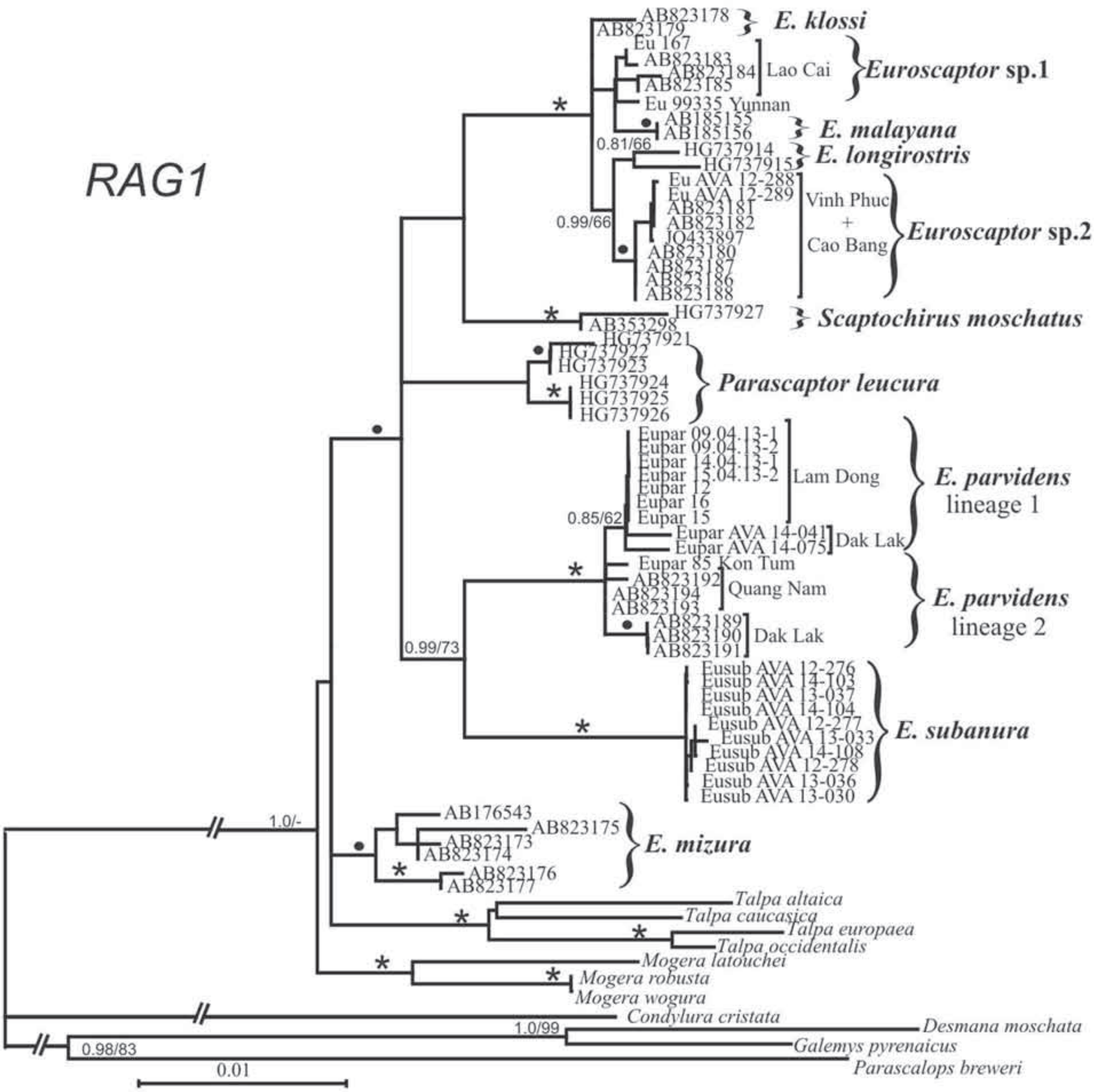


Fig. 4. ML gene trees for *Euroscaptor* produced by separate analyses of the fragments of *RAG1, A2ab, BRCA1, BRCA2* and *ApoB*. The asterisks denote the nodes that are highly supported in all analyses (Bayesian posterior probabilities (BPP) >0.95, ML bootstrap support >90%), filled circles mark moderately supported nodes (Bayesian posterior probabilities (BPP)>0.85, ML>70%).

ever, the resolution of branches within these clades is not as clear as that in the mitochondrial tree.

In the first clade, *Euroscaptor* sp.1 and *Euroscaptor* sp.2 do not form a monophyletic group. The Vietnamese sample from Lao Cai and the specimen from Yunnan (*Euroscaptor* sp.1) are weakly grouped with *E. malayana*. The GenBank specimens of *E. longirostris* from Sichuan are joined with Vietnamese sample from Cao Bang and Vinh Phuc (*Euroscaptor* sp.2) also being weakly supported by the BI and ML analyses. The nuclear DNA of *E. longirostris* from Sichuan (Mouping) is presented in GenBank only by

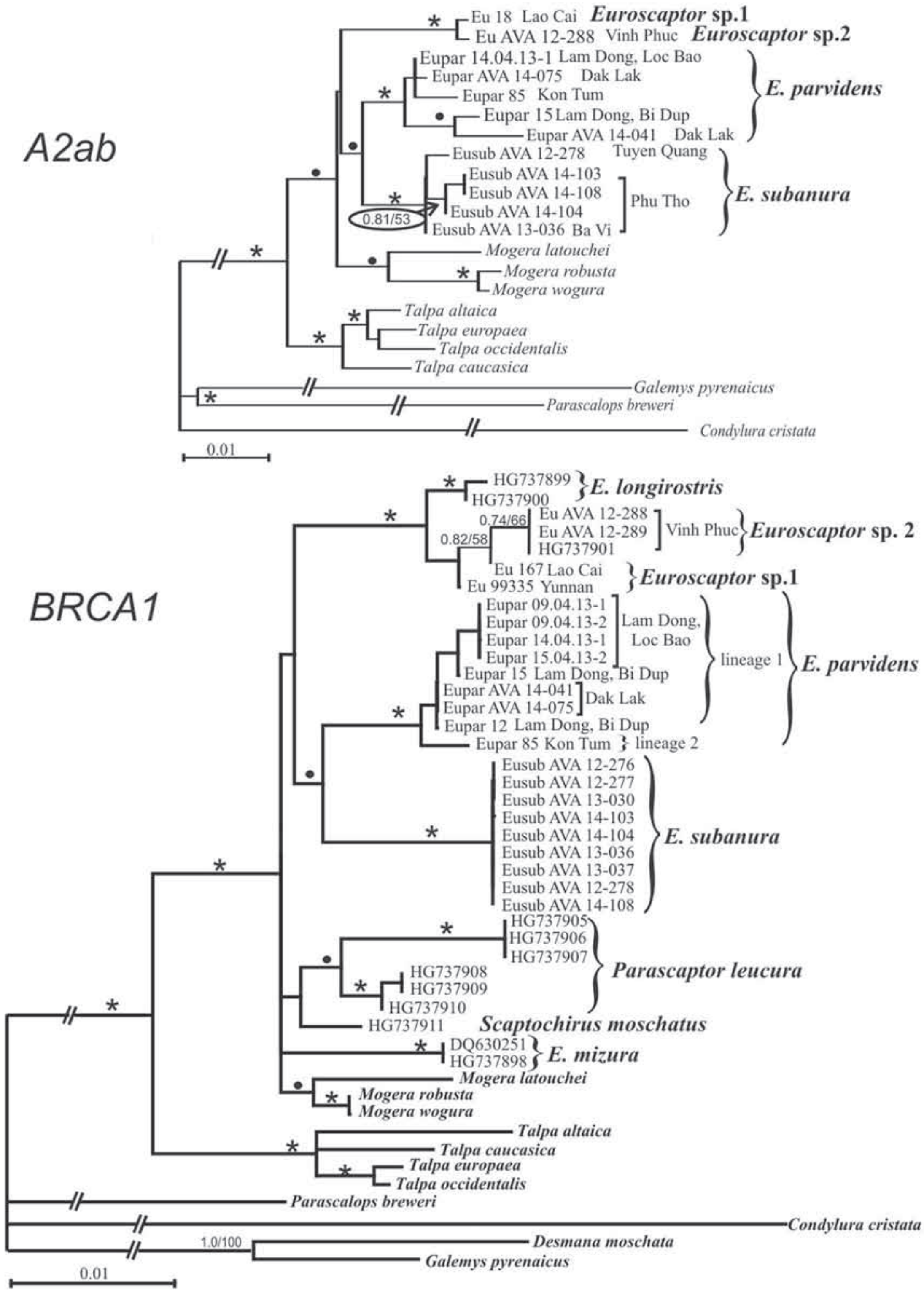


Fig. 4 (continued).

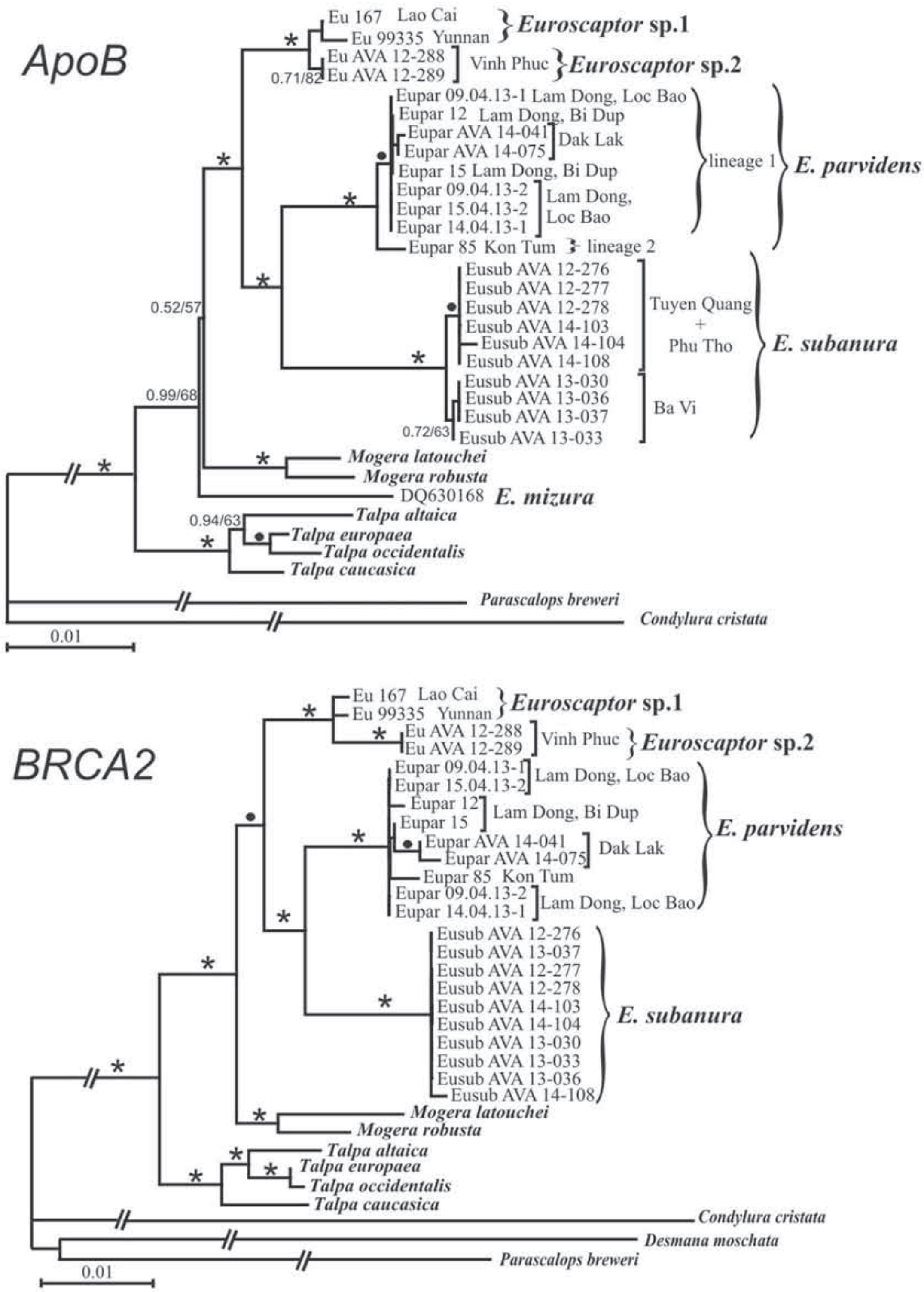


Fig. 4 (continued).

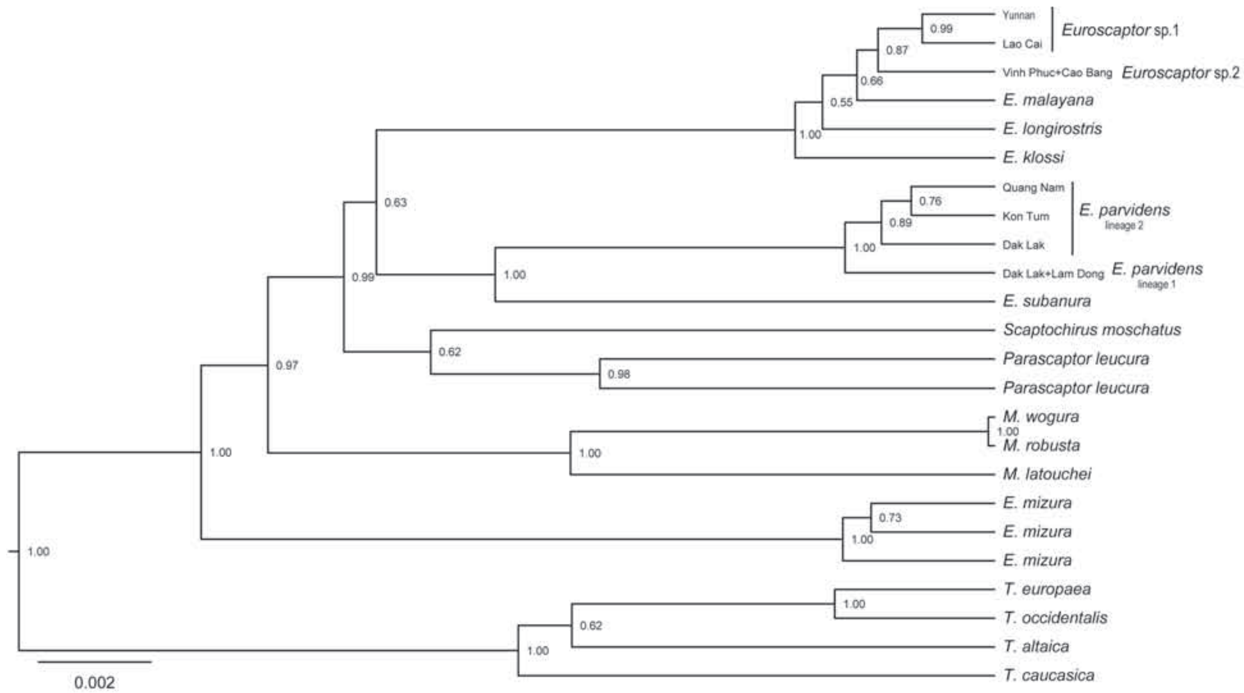


Fig. 5. Species tree of *Euroscaptor* produced by the *BEAST algorithm using the Bayesian multispecies coalescent approach. Values above the branches correspond to Bayesian posterior probabilities.

Table 2. Factor loadings and explained variance for the principal components PC1 and PC2 in the PCA (Fig. 6); canonical correlations and explained variance for the canonical axes CAN1 and CAN2 in the DFA (Fig. 7).

Characters	PC 1	PC 2	CAN 1	CAN 2
GLS	-0.907	0.276	-0.102	-0.384
CBL	-0.908	0.285	-0.098	-0.354
PL	-0.950	0.076	-0.039	-0.391
LZA	-0.387	0.793	-0.301	-0.192
I1-M3	-0.958	-0.200	0.055	-0.422
C-M3	-0.913	-0.285	0.081	-0.398
M1-M3	-0.795	-0.371	0.072	-0.257
RB	-0.354	0.778	-0.203	-0.066
BIOF	-0.714	0.312	-0.046	-0.169
BAM	-0.776	0.097	0.012	-0.278
IOB	-0.482	-0.104	0.019	-0.054
BCW	-0.870	0.239	-0.090	-0.469
BH	-0.748	-0.107	-0.014	-0.332
ML	-0.930	0.222	-0.084	-0.442
MH	-0.829	0.073	-0.031	-0.296
i1-m3	-0.915	-0.292	0.070	-0.392
p1-m3	-0.867	-0.443	0.159	-0.455
m1-m3	-0.806	-0.507	0.165	-0.345
Explained variance (%)	64.7	13.5	55.6	28.3

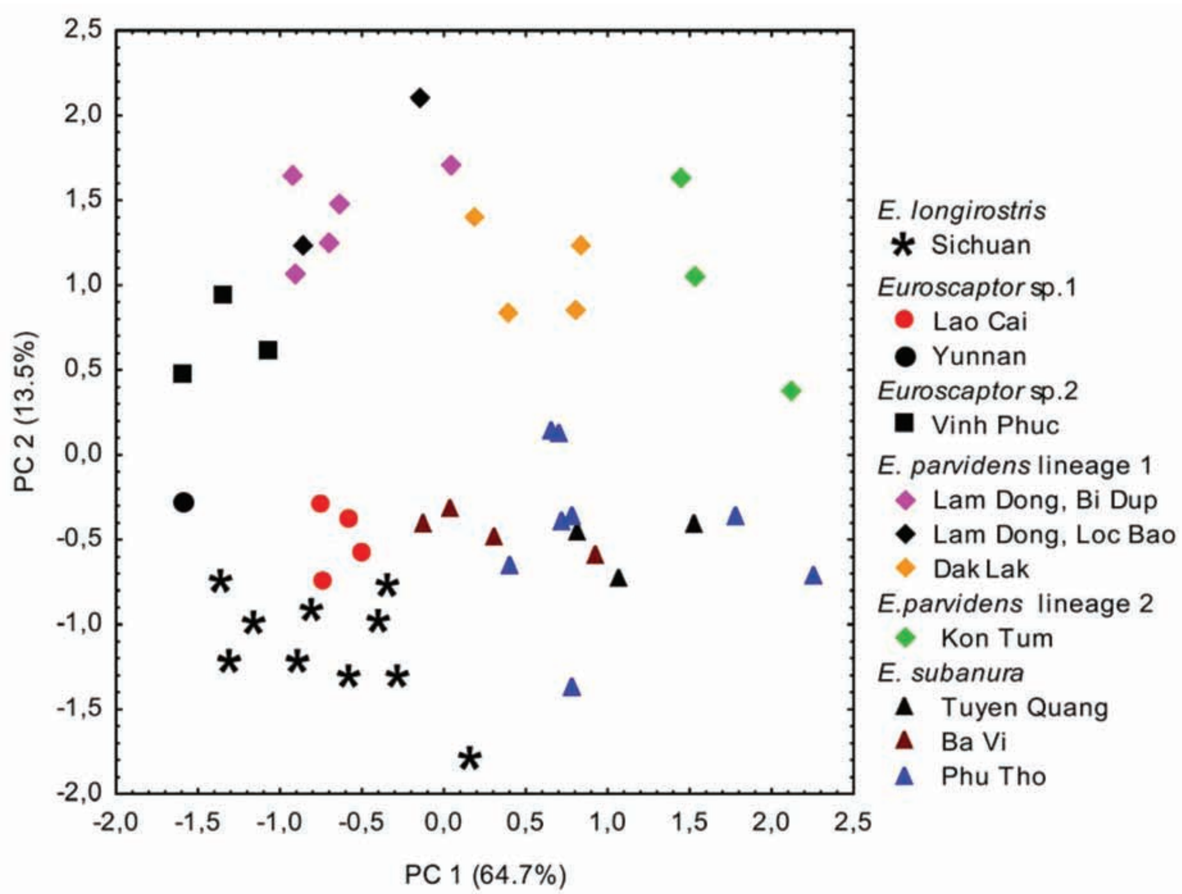


Fig. 6. Ungrouped morphometric separation (principal components analysis) of *Euroscaptor* spp.

the sequence of RAG1 (Fig. 4), which does not group it with the RAG1 sequences of *Euroscaptor* sp.1 and *Euroscaptor* sp.2.

In the lineage of *E. parvidens* s.l. + *E. subanura*, the split of specimens from northern and central Vietnam is not as clear as in the mitochondrial tree.

The lineage 1 of *E. parvidens* from southern Vietnam (Lam Dong, Dak Lak) form a monophyletic group, however the support of lineage 2 (the samples from Kon Tum and Quang Nam) is absent on the nuclear tree. The specimens from Dak Lak are not united in one group: whereas our sample belongs to *E. parvidens* s.str., three specimens from GenBank form a separate branch.

Species tree estimation

The species tree inferred by using *BEAST (Fig. 5) reproduces the topology of the five-gene nuclear phylogenetic tree. The deviation from the topology of the mitochondrial tree concerns only the low supported branches. The relationships within *Euroscaptor* (except for *E. mizura*) are again resolved in favour of two major clades: the highly supported sister relationships between *E. parvidens* and *E. subanura* on the one hand, and *E. klossi, E. malayana, E. longirostris* from Mouping and *Euroscaptor* spp. from northern Vietnam and southern China on the other hand. *Scaptochirus moschatus* forms a sister branch to *Parascaptor leucura* s.l. The basal position of *E. mizura* relative to all other moles of Southeast Asia is highly supported.

Morphometric analysis

Results of the PCA of craniometric characters in the revealed genetic clusters are shown in Fig. 6 and Table 2. As inferred from the scatterplot, *E. parvidens*

comprises three groups corresponding to the geographical distribution of studied specimens: (1) Kon Tum, (2) Dak Lak, and (3) Lam Dong (Loc Bao and Bi Dup). The three groups diverge along the first principal component PC 1, in particular reflecting differences in the overall cranial size. The specimens from Kon Tum show the smallest average meanings of skull measurements, whereas those from Lam Dong – the largest one. Moles of *E. longirostris* group (sensu lato) were separated from each other mostly along the second principal component PC 2, but overlapped to some degree. The specimens from Sichuan regarded as *E. longirostris* could be diagnosed by the low PC 1 and PC 2 scores in this plot. Within *Euroscaptor* sp.1 differences in PC 1 between samples from Lao Cai and Yunnan have been found. The position of *Euroscaptor* sp.2 was separated from the other two *E. longirostris* group species based on a relatively high value of PC 2, corresponding to the rostral breadth and length of the zygomatic arch. The morphometric differentiation in *E. subanura* has not been revealed.

DFAs drawing on the same variables have provided another means of illuminating the morphometric distinctions between Vietnamese moles (Fig. 7, Table 2). The discrimination between taxa of *E. longirostris* group has been most strongly based upon the first canonical axis CAN 1, while *E. subanura* and *E. parvidens* lineage 2 (Kon Tum) diverged from other taxa along the second canonical axis, in particular reflecting its small size.

DISCUSSION

Phylogenetic relationships among Euroscaptor

Several contradicting hypotheses on phylogenetic relationships among *Euroscaptor* species have been advanced. Stroganov (1948) placed *longirostris* and *micrura* in the separate genus *Eoscalops* Stro-

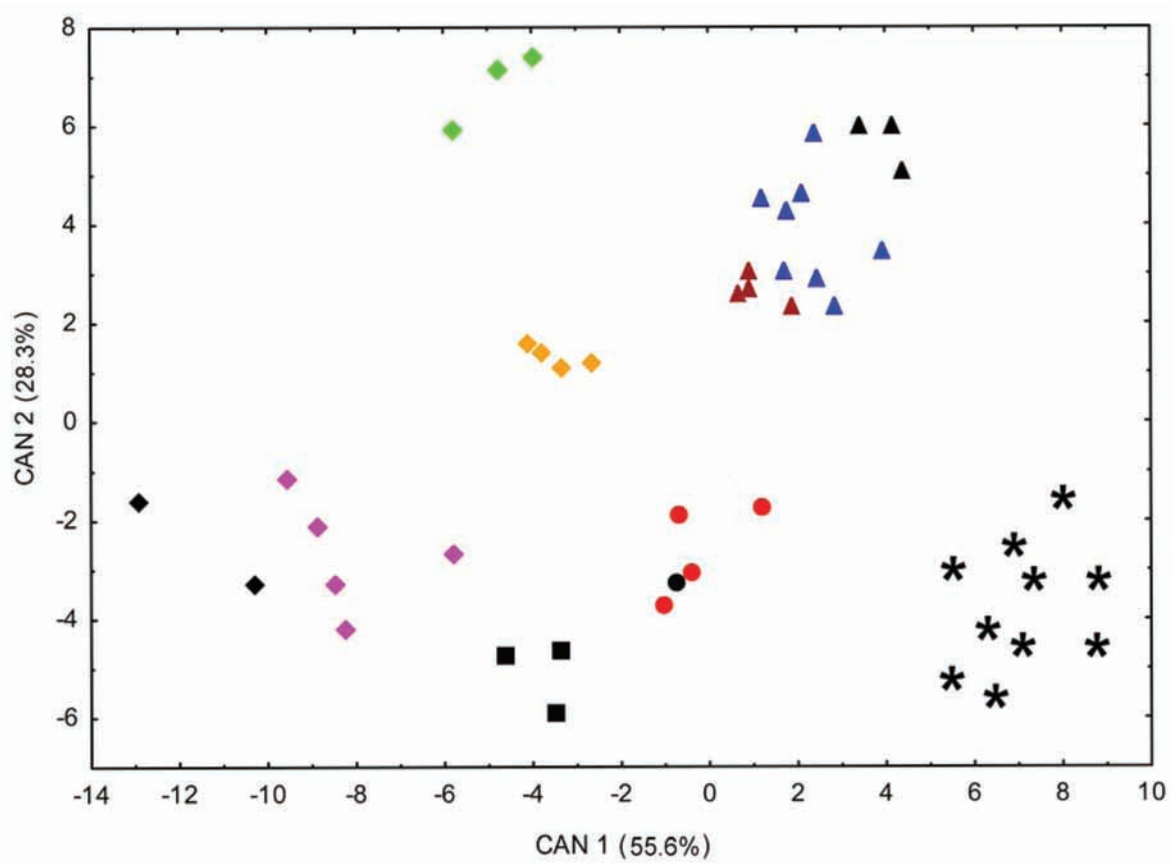


Fig. 7. Grouped morphometric separation (discriminant function analysis) drawn from the same specimens and measurements for *Euroscaptor* spp. as in Fig. 6. Symbols as in Fig. 6.

ganov, 1941, whereas other species (*grandis*, *klossi* and *parvidens*) considered in the genus *Euroscaptor*. Pavlinov (2003) distinguished two distinct species groups in *Euroscaptor*: the «*longirostris*»-group with the only species *E. longirostris* and the «*micrura*»-group that included all other species. Based on cranial and dental (relative length of upper molar rows) characters, Kawada et al. (2009) recognized two groups in *Euroscaptor* – *E. grandis*, *E. klossi*, *E. malayana*, *E. micrura* (and *E. mizura*) have skulls of the «*klossi*-type», whereas *E. longirostris* and *E. parvidens* have skulls of the «*longirostris*-type».

Contrary to these hypotheses, our data indicate the occurrence of two monophyletic lineages in *Euroscaptor* s.str. (without *E. mizura*). The eastern lineage includes two Vietnamese forms (*parvidens* and *subanura*), whereas the western lineage includes all other taxa (*longirostris*, *malayana*, *klossi*, sp.1 and sp.2). He et al. (2014) found out that the timing of divergence among these lineages could coincide with the *Parascaptor*/*Scaptochirus* split. A divergence between the eastern and western lineages of *Euroscaptor*-like moles seems to reflect a colonization history of South Asia. The widely distributed western lineage could have rapidly dispersed throughout southern Asia, from China to Malaysia, in the late Miocene (He et al. 2014), whereas the eastern lineage can represent the descendants of the first radiation that survived in the refugees of eastern Indochina. Uplifting of mountains and isolation by large rivers could result in further speciation. However, it is necessary to study populations from India and western Indochina in order to infer a complete evolutionary history of this group, which will be a subject of a forthcoming study.

Species diversity: general remarks

The present study based on mitochondrial and nuclear DNA covering a wide distribution of Vietnamese moles has substantially extended the knowledge of genetic variation in *Euroscaptor* of this region. It has been found that the genus *Euroscaptor* is characterized by a high cryptic diversity. The genetic lineages which have been found for the known species have a clear geographical confinement. The essential mitochondrial genetic distances between these lineages (6–9%) often correspond to those between pairs of the sister species in other groups of the strictly fossorial moles such as *Talpa* or *Mogera* (Tsuchiya et al. 2000; Bannikova et al. 2015). The phylogeographic breaks found within the *Euroscaptor* species correlate with the definite geographical barriers that could block gene exchange between the phylogroups. It is known that moles of the genus *Euroscaptor* are distributed in the mountain areas, and do not occur in sympatry (Abe 1967). The only case is the *Euroscaptor* sp.2 (listed as *E. longirostris*) and *E. subanura* in Tam Dao, however, these species are really parapatric because they are separated by altitudinal confinement (Kawada et al. 2012; Abramov et al. 2013a). The tendency to allopatric or parapatric distribution is known in other strictly fossorial moles of the genera *Talpa* or *Mogera* (Mitchell-Jones et al. 1999; Hutterer 2005). In Vietnam, different phylogroups of moles are associated with different mountain systems or separated by Red River. It is worth mentioning that in some cases the revealed intraspecific genetic forms also possess specific morphological (external and cranial) features.

The pattern of genetic variation in the genus *Euroscaptor* revealed in the present study suggests the existence of several cryptic lineages that could be treated as distinct species based on their genetic and morphological distinctness and geographical distribution. In the following sections we shall provide a brief discussion of the taxonomic status of the genetically and morphologically distinct lineages of *Euroscaptor* species occurring in Vietnam and south Asia and formally describe two new species and one new subspecies.

Taxonomic implications

E. longirostris lineage

Both genetic and morphological data attest to the existence of cryptic species diversity within the currently recognized *E. longirostris* and are in agreement with the data by He et al. (2014) who reported on the intraspecific variability between samples from Sichuan and northern Vietnam (Tam Dao). The studied specimens from Sichuan, including one from the type locality of *E. longirostris*, are clearly different from those from the North Vietnamese and Yunnan that were hitherto attributed to this species. Based on the orography of this region, one can assume that the distribution of true *E. longirostris* is restricted to Sichuan, northward of Yangtze River. The populations found southward of this isolation barrier

evidently represent a new species *Euroscaptor* sp.1. The aforementioned significant differences between moles from northwestern and northeastern Vietnam strongly corroborate their species rank. Red River which divides the western and eastern parts of northern Vietnam beyond doubt isolates the *Euroscaptor* sp.1 and *Euroscaptor* sp.2 populations. This assumption is in full agreement with the conclusion by Bannikova et al. (2011) who argued that Red River forms a distribution barrier between some *Crocidura* species.

One of the Sichuan specimens (KIZ 0905172) originated from the type locality of *E. longirostris* (Baoxing, formerly Mouping), another one (KIZ 0905290) was collected from Omei Mt., which is the terra typica for *E. grandis* Miller, 1940. The latter was described from the single specimen (USNM 255370) that was distinguishable by its large size (GLS=37 mm). The specimens from KIZ have GLS 33.4 and 30.7 mm, i.e. within the size range of *E. longirostris*. As argued above, a sympatric occurrence of *Euroscaptor* species seems unlikely, and thus it is safe to consider the taxonomic status of *E. grandis* as yet obscure; it could be either an aberrant form of *E. longirostris*, or, if not, its type locality was mistakenly recorded. According to the field notebook of D.C. Graham who collected the type specimen in 1930, this large mole was purchased in Kiating (now Leshan). Graham fixed the locality as "Mount Omei, Szechuan, China, at an altitude of 5000 feet" based on the information obtained from local hunters. Perhaps the real collecting locality of *E. grandis* was different. More sampling in Omei Mt. region is needed to resolve this matter.

E. parvidens lineage

A genetic differentiation of the populations of *E. parvidens* from southern and central Vietnam is highly pronounced, as revealed from the mitochondrial *cytb* gene and nuclear DNA analyses. The populations of Dalat Plateau, including the samples from Loc Bao, Bi Dup and Chu Yang Sin, form a well-supported clade and can be attributed to true *E. parvidens*. This species was described from Di Linh located 40–45 km NW of our collecting site Loc Bao in Bao Lam District of Lam Dong, Vietnam (Fig. 1). The specimens from central Vietnam (Kon Tum and Quang Nam) are significantly different from them, yet, the monophyly of this group is supported by the mtDNA only. This fact makes it difficult to recognize this clade as a separate taxon of species rank. Meanwhile, moles from the two lineages of *E. parvidens* differ in their morphology (viz., body and skull sizes, the shape of P4). The populations of Kon Tum and Quang Nam are rather distinct from that of Dalat Plateau and undoubtedly represent a new subspecies that is described below. It is worth mentioning that the high mountains of Kon Tum Plateau including Ngoc Linh Mt. bear a high endemic diversity of vertebrates. Ngoc Linh Mt. is known as a locality for such endemic species as shrew *Crocidura sokolovi* (Jenkins et al. 2007), frogs *Vibrissaphora ngoclinhensis* and *Gracixalus lumarius* (Orlov 2005; Rowley et al. 2014), snake *Calamaria abramovi* (Orlov 2009), and barwing *Actinodura sodangorum* (Eames et al. 1999).

The situation in Dak Lak (Chu Yang Sin, localities 7 and 15 in Fig. 1) where both lineages are presented remains unclear. It is hardly possible to make any conclusion about possible reasons for this genetic diversity in Chu Yang Sin area, since we know nothing about the specimens by Shinohara et al. (2014) of which sequences were presented in GenBank.

The studied genetic data (see above) support a close affinity of the recently described *E. subanura* and *E. parvidens*, as it was argued by Kawada et al. (2012) on the basis of morphological analysis. Nevertheless, *E. subanura* well differs both morphologically and genetically from the *parvidens* lineage. The studied samples of *E. subanura* show low genetic variability, despite their wide geographic range. Such a low genetic diversity may be indicative of recent colonization of these populations across the most part of their distribution range during a short period of time. A recent colonization of *E. subanura* in Vietnam could result from a late expansion event northward to the areas that were already occupied by members of the *longirostris* lineage. Most of the high elevation areas in this region were already occupied by *longirostris*-like moles, therefore *E. subanura* could expand to low elevations only. In Tam Dao Mt., this species is distributed at the elevations of 200–300 m a.s.l. and another species of the *longirostris* group occurs at the higher elevations of 700–1000 m a.s.l. (Kawada et al. 2012). However, in the area where no sympatic species occur, *E. subanura* can occupy a higher elevation; for example, in Ba Vi this species occurs at the elevations of 300–1000 m a.s.l. (Abramov et al. 2013b).

Western moles

A taxonomic diversity of the moles from western Indochina and India remains poorly studied. The Malayan mole *E. malayana* and *E. klossi* from Thailand appear to be genetically close to the *longirostris*-lineage. Shinohara et al. (2014) estimated that the diversification of this group (*klossi*, *malayana* and *longirostris* s.l.) took place ca. 5.3 Mya (3.8–7.9 Mya).

The phylogenetic relationships of *E. micrura* and *E. cryptura* from the western Himalayas with other Asian moles are still unstudied. These large-sized moles with very short tails are known from Nepal and northern India. Their distribution ranges are isolated from the studied mole lineages by great Brahmaputra and Irrawaddy Rivers, so these taxa are likely to represent very different genetic lineages. Motokawa (2004) conducted a phylogenetic analysis of members of the family Talpidae and came to the conclusion that *micrura* and *longirostris* form two paraphyletic groups.

SYSTEMATICS

Genus *Euroscaptor* Miller, 1940

Type species: *Talpa klossi* Thomas, 1929.

Distribution: widely distributed in South Asia, occurring in China, Nepal, Laos, Vietnam, Myanmar, Thailand, and Peninsular Malaysia.

Composition: *Euroscaptor klossi* (Thomas, 1929), *Euroscaptor longirostris* (Milne-Edwards, 1870), *Euroscaptor malayana* (Chasen, 1940), *Euroscaptor parvidens* (Miller, 1940), *Euroscaptor subanura* Kawada et al., 2012, *Euroscaptor orlovi* sp. nov., and *Euroscaptor kuznetsovi* sp. nov. (see descriptions below). Probably, also includes *Euroscaptor grandis* Miller, 1940 and *Euroscaptor micrura* (Hodgson, 1841). The taxonomic status of *"Talpa" cryptura* Blyth, 1843 from Darjeeling, India remains obscure.

Euroscaptor orlovi sp. nov.
(Figs 8B, 10B)

Holotype. ZIN 96318, collector's number 18, female, body in ethanol, skull extracted, VIETNAM, Lao Cai Province, 6 km W of Sa Pa, north slope of Fansipan Mt. area, near Tram Ton forest station, 22°21´N, 103°46´E, altitude 2000 m a.s.l.; collected 10 December 2005 by A.V. Abramov.

Paratypes. ZIN 98142, collector's number 146, sex unknown, body in ethanol, skull extracted, collected 31 May 2006 by A.V. Abramov; ZIN 97789, collector's number 167, male, body in ethanol, skull extracted, collected 30 May 2008 by A.V. Abramov and A.V. Shchinov; ZIN 101559, collector's number 80, female, body in ethanol, skull extracted, collected 7 March 2012 by A.V. Shchinov; all from the same locality as the holotype.

Other material. BMNH 33.4.1.148, female, skull, Chapa (= Sa Pa, Lao Cai Province, Vietnam); ZIN 99335, sex unknown, body in ethanol, skull extracted, Jingdong County, Yunnan Province, China.

Diagnosis. Large-sized mole, comparable to *E. longirostris*. Pelage blackish brown. Tail long and club-shaped. Rostral part of skull elongated and narrow. Posterolingual border of P4 deeply concave. Anterior parts of auditory bullae flatted and straddling. A new species distinguished by the mitochondrial gene cytochrome *b* and five nuclear genes (*BRCA1*, *BRCA2*, *ApoB*, *RAG1* and *A2ab*) (see Figs 2–4).

Description and comparisons. Head and body length 115–129 mm, with a long tail, 12.6–13.7% of head and body length. Tail club-shaped, evenly covered with long overhairs. Dorsal and ventral pelage blackish brown. Body elongated. Skull with a long and narrow rostrum (see Fig. 8B). All upper premolars with 2 roots, in P2 roots often adnated, P2 smaller than P1, P3 much wider them. P1 narrow, without metastyle. P4 with small parastyle, talon of a moderate size, shorter than metastyle part, the posterolingual border of the tooth deeply concave (Fig. 10B). The coronoid process with a narrow apex. Condyle-angular region of mandible not oblong.

Tail long and club-shaped unlike short, bulb-shaped tail in *E. parvidens* and *E. subanura*. New species differs from *E. kuznetsovi* sp.nov. in the slightly smaller and light-built skull with a relatively narrow rostral part. Angular process long, band-shaped, with a relatively narrow base; in *E. kuznetsovi* sp. nov., this base wider and process looks triangular. The new species is similar in size with *E. longirostris*, but differs in having short toothrows. Larger on average than *E. parvidens* and *E. subanura*, with a longer tail. Anterior parts of auditory bullae flatted and straddling concave in *E. orlovi* sp. nov., *E. kuznetsovi* sp. nov., and *E. longirostris*, but it inflated and converge in *E. parvidens* and *E. subanura*. Posterolingual border of P4 deeply concave in *E. orlovi* sp. nov., *E. kuznetsovi* sp. nov. and *E. longirostris*, but it shallowly concave in

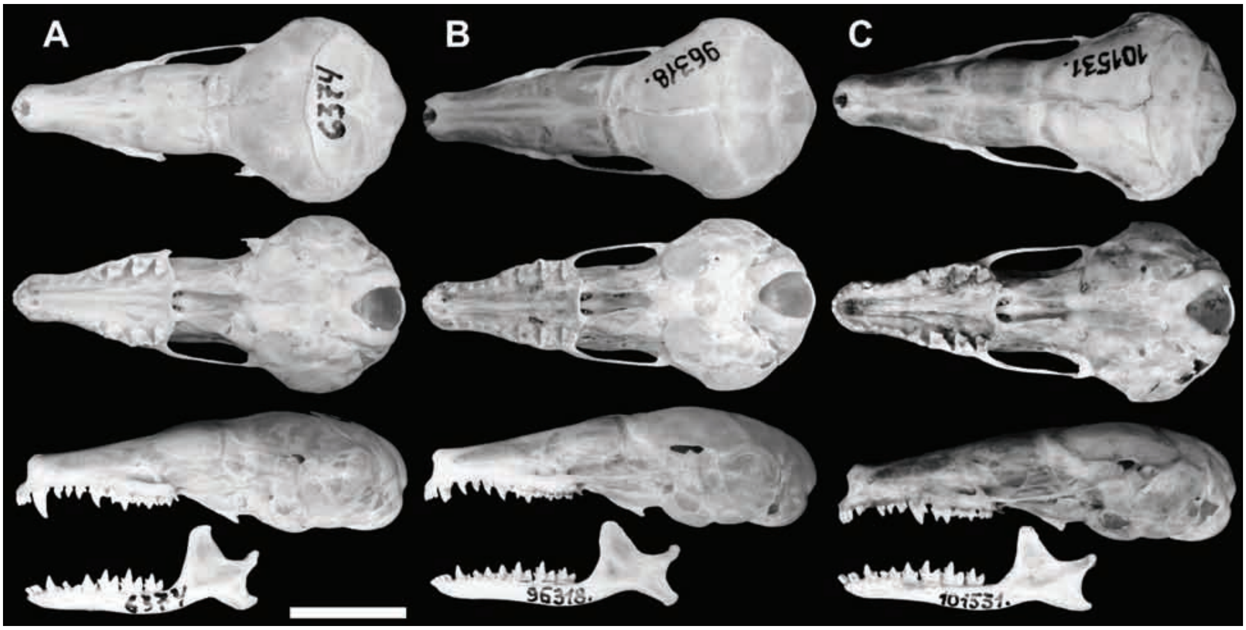


Fig. 8. Dorsal, ventral and lateral views of skull, and mandible of *Euroscaptor*. A – *E. longirostris* (ZIN 6374, China, Sichuan), B – *E. orlovi* sp.nov. (ZIN 96318, holotype, Vietnam, Sa Pa), C – *E. kuznetsovi* sp. nov. (ZIN 101531, holotype, Vietnam, Tam Dao). Scale bar = 10 mm.

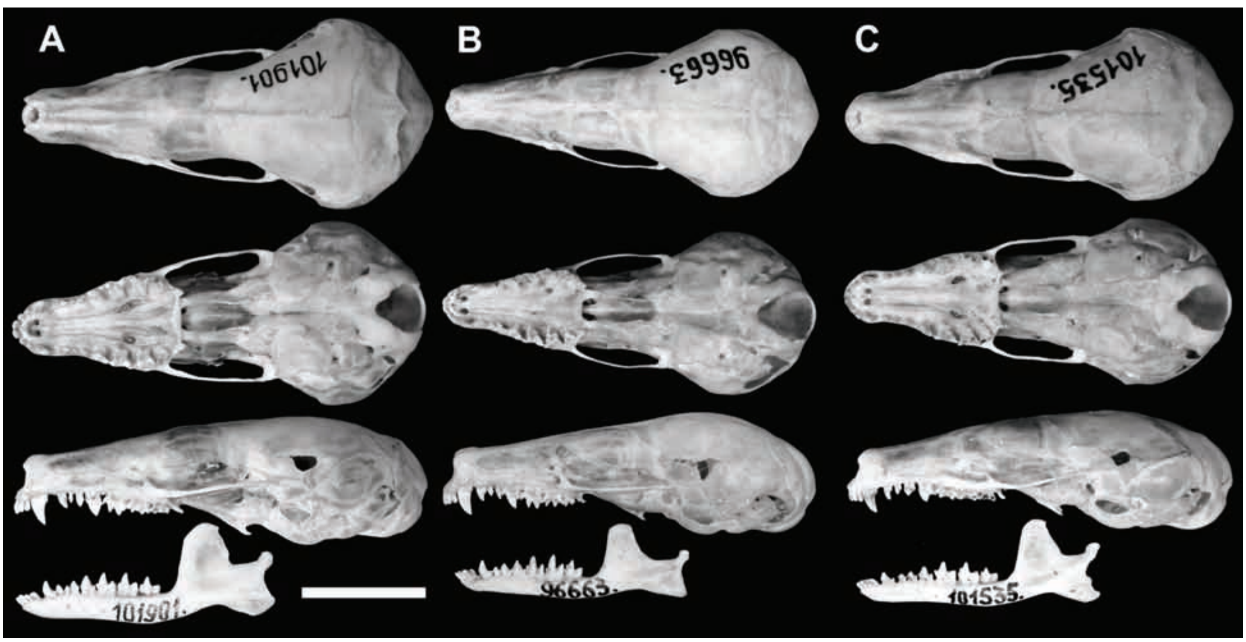


Fig. 9. Dorsal, ventral and lateral views of skull, and mandible of *Euroscaptor*. A – *E. parvidens* (ZIN 101901, Vietnam, Loc Bao), B – *E. parvidens ngoclinhensis* ssp.n. (ZIN 96663, holotype, Vietnam, Ngoc Linh), C – *E. subanura* (ZIN 101535, Vietnam, Vuoc Ly). Scale bar = 10 mm.

E. parvidens and *E. subanura* (Fig. 10). The coronoid process with a narrow apex, similar to *E. kuznetsovi* sp. nov. and *E. longirostris*, whereas it short, with a wide apex in *E. parvidens* and *E. subanura* (see Figs 8–9).

Etymology. The new species is named in honour of Dr. Nikolai L. Orlov (Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia) in recognition of his remarkable contributions to the study of animals of Vietnam.

Distribution. Found in northern Vietnam (Lao Cai Province, Sa Pa District) and southern China (Yunnan Province). It may have a wider distribution in the highlands of northern Laos and in northwestern Vietnam, probably westward of Red River.

Remarks. The species is reported as *Euroscaptor* sp. 1 in the results of both genetic and morphological analyses.

Euroscaptor kuznetsovi sp. nov.

(Figs 8C, 10C)

Type locality.

Holotype. ZIN 101531, collector's number AVA 12–288, male, body in ethanol, skull extracted, VIETNAM, Vinh Phuc Province, vicinity of Tam Dao, 21°27´06´´N, 105°38´09´´E, altitude 750 m a.s.l.; collected 24 November 2012 by A.V. Abramov.

Paratypes. ZIN 101532, collector's number AVA 12–289, male, body in ethanol, skull extracted, collected 25 November 2012 by A.V. Abramov; ZMMU S–161162, male, skin, skull, collected 6 February 1993 by G.V. Kuznetsov; both specimens from the same locality as the holotype.

Diagnosis. Large-sized mole, comparable to *E. longirostris* and *E. orlovi* sp. nov. Pelage blackish brown. Tail long and club-shaped. Rostral part of skull elongated and relatively wide. Posterolingual border of P4 deeply concave. Anterior parts of auditory bullae flatted and straddling. A new species distinguished by the mitochondrial gene cytochrome *b* and five nuclear genes (*BRCA1*, *BRCA2*, *ApoB*, *RAG1* and *A2ab*) (see Figs 2–4).

Description and comparisons. Head and body length 132–136 mm, with a long tail, 11.4–12.5% of head and body length. Tail club-shaped, evenly covered with long overhairs. Dorsal and ventral pelage blackish-brown. Body elongated. Skull with a long and narrow rostrum (Fig. 8C). All upper premolars with 2 roots, P1 and P2 similar in height, P3 much wider them. P1–P2 with metastyles. P4 with small parastyle, talon of a moderate size, shorter than metastyle part, the posterolingual border of the tooth deeply concave (Fig. 10C). The coronoid process with a narrow apex. Condyle-angular region of mandible not oblong.

Tail long and club-shaped unlike short, bulb-shaped tail in *E. parvidens* and *E. subanura*. New species differs from *E. longirostris* in the larger skull size and relatively short molar rows. Larger on average than *E. parvidens* and *E. subanura*. It differs from *E. longirostris* and *E. orlovi* sp. nov. in their relatively wide rostral part of the skull, however it much wider in *E. malayana* and *E. klossi*. The new species has P1 and P2 similar in height, whereas in *E. orlovi* sp. nov. and *E. longirostris* P1 larger than P2. Posterolingual

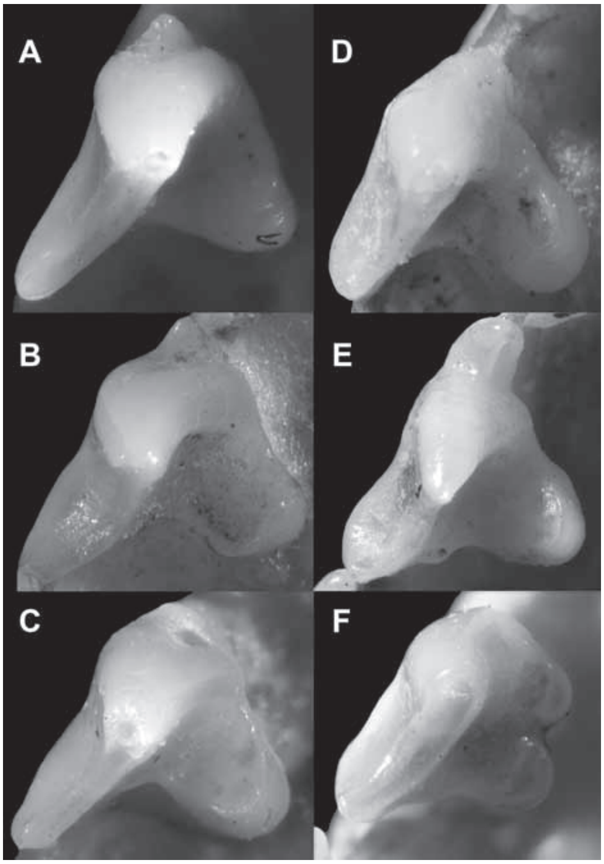


Fig. 10. Upper fourth premolar in SE Asian moles. A – *E. longirostris* (ZIN 6374, China, Sichuan), B – *E. orlovi* sp. nov. (ZIN 96318, holotype, Vietnam, Sa Pa), C – *E. kuznetsovi* sp. nov. (ZIN 101531, holotype, Vietnam, Tam Dao), D – *E. parvidens* (ZIN 101901, Vietnam, Loc Bao), E – *E. parvidens ngoclinhensis* ssp.nov. (ZIN 96663, holotype, Vietnam, Ngoc Linh), F – *E. subanura* (ZIN 101535, Vietnam, Vuoc Ly). Scale bar = 10 mm.

border of P4 deeply concave in *E. kuznetsovi* sp. nov., *E. orlovi* sp. nov., and *E. longirostris*, but it shallowly concave in *E. parvidens* and *E. subanura* (Fig. 10). Anterior parts of auditory bullae flatted and straddling concave in *E. kuznetsovi* sp. nov., *E. orlovi* sp. nov. and *E. longirostris*, but it inflated and converge in *E. parvidens* and *E. subanura*. The coronoid process is narrow, differing markedly in shape from that of *E. parvidens* and *E. subanura* (see Fig. 9).

Etymology. The new species is named in honour of Dr. German V. Kuznetsov (A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow) in recognition of his many contributions to the study of mammals of Vietnam.

Distribution. Distributed in north-eastern Vietnam. It is recorded from Vinh Phuc Province (Tam Dao) and Cao Bang Province (Nguyen Binh District). Found at the elevations of 750–950 m a.s.l. Probably, the record from Guangxi, south-eastern China (Hoffman and Lunde 2008) belongs to this species as well.

Remarks. The species is reported as *Euroscaptor* sp. 2 in the results of both genetic and morphological analyses.

Euroscaptor parvidens ngoclinhensis **subsp. nov.**
(Figs 9B, 10E)

Holotype. ZIN 96663, collector's number 33, female, body in ethanol, skull extracted, VIETNAM, Kon Tum Province, Dac Glei District, 2–3 km W of Ngoc Linh Mt., 15°05´N, 107°57´E, altitude 1700–1750 m a.s.l.; collected 26 March 2006 by A.V. Abramov.

Paratypes. ZIN 96664, collector's number 84, female, body in ethanol, skull extracted; ZIN 96665, collector's number 85, female, body in ethanol, skull extracted, collected 7 April 2006 by A.V. Abramov from the same locality as the holotype.

Diagnosis. Small-sized mole, comparable only to *E. subanura*, and smaller on average in its external and cranial measurements than the nominotypical *E. parvidens*. The fourth upper premolar with a well developed parastyle. A new species distinguished by the mitochondrial gene cytochrome *b* (see Fig. 2).

Description and comparisons. Head and body length 120–123 mm, with a short tail, 5.8–6.1% of head and body length. Tail bulb-shaped, covered with long overhairs. Dorsal and ventral pelage dark brown. Body elongated with rump greatly enlarged posteriorly. Skull (Fig. 8 B) with a long and moderately wide rostrum. Upper and lower toothrows short. The upper premolars P1 and P3 similar in height and have 2 roots, P2 much smaller them and has one root. P1–P3 with remarkable metastyles. P4 with well-developed parastyle, talon wide and similar in size with metastyle part, the posterolingual border of the tooth shallowly concave (Fig. 10). The coronoid process short, with a wide apex. The angular process well-developed, with a wide base. Condyle-angular region of mandible oblong.

New subspecies differs from the nominotypical *E. parvidens* in the smaller body and skull sizes and in the relatively short upper and lower toothrows. The parastyle of P4 is weakly developed in *E. parvidens*. P1 in *E. parvidens parvidens* is narrow, without metastyle, whereas in *E. parvidens ngoclinhensis* ssp. nov. the tooth is similar in width to P3 and has metasyle. In *E. subanura*, P4 has a well-developed additional tubercle located anteriorly to protocone (Fig. 10F), which absent from both subspecies of *E. parvidens*.

Etymology. The subspecies is named after the Ngoc Linh Mountain in Kon Tum Province of Vietnam, from where it was collected for the first time.

Distribution. Known from the Central Highlands of Vietnam (Kon Tum and Quang Nam provinces). Probably, the moles from Gia Lai Province (Abramov et al. 2013a) belong to this subspecies.

Remarks. The species is reported as *Euroscaptor parvidens* lineage 2 in the results of both genetic and morphological analyses.

ACKNOWLEDGEMENTS

We are thankful to Ms. Olga Makarova (ZIN) and Dr. Paulina Jenkins (BMNH) for giving access to the collections under their care. We thank all people who provided samples for this study. We thank Prof. Wang Yingxiang and Dr. Kai He for providing us with the useful information about specimens from KIZ. We are very grateful to Dr. Rainer Hutterer, Dr. Shin-ichiro Kawada, Dr. Boris Sheftel, Dr. Leonid Voyta and three anonymous reviewers for their helpful comments on the early version of the manuscript. Fieldworks in Vietnam were possible due to the support of the Joint Vietnam-Russian Tropical Research and Technological Centre. We thank Dr. Andrey Kuznetsov, Anton Shchinov, Dr. Nguyen Dang Hoi, Pham Duc Tien, Tran Quang Tien for their great help during fieldworks. We also thank the administrations and forest rangers of Bi Dup – Nui Ba, Ba Vi, Hoang Lien, Chu Yang Sin, Ngoc Linh and Xuan Son national parks for their aid in the management of our studies. Dr. Dmitri Logunov (Manchester Museum,

UK) is thanked for improving the English of the first draft. We are very grateful to anonymous reviewers for their helpful and constructive comments on the manuscript. The study was supported in part by the RFBR grants 14-34-50760, 13-04-00525 and 16-04-00085 (collection of material and the processing of the paper), 14-04-00034a, 15-29-0277ofi-m (genetic studies), and Russian Science Foundation, project 14-50-00029 (phylogenetic analysis and the processing of the paper).

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Submitted April 8, 2016; accepted May 10, 2016.

Appendix 1. List of the GenBank accession number of DNA sequences used in phylogenetic analysis. For SE Asian *Euroscaptor* the geographic information and locality code (Fig.1) are provided.

Euroscaptor longirostris:

China, Sichuan Province, Baoxing (=Mouping) and Emei Mt. (He et al. 2014), locality 12 in Fig. 1: HG737870, HG737871 [*cytb*]; HG737914, HG737915 [*RAG1*]; HG737899, HG737900 [*BRCA1*].

Euroscaptor sp.1:

Vietnam, Lao Cai Province, 6 km west of Sa Pa, north slope of Fansipan Mt., near Tram Ton forest station, 22°21´N, 103°46´E (Zemlemerova et al. 2013), locality 1 in Fig.1: KC481345, KC481346, KC481347 [*cytb*]; KC481369 [*RAG1*]; KC481357 [*BRCA1*]; KP717146 [*BRCA2*]; KP717258 [*ApoB*]; KP995409 [*A2ab*];

Vietnam, Lao Cai Province, Sapa (Shinohara *et al.* 2014), locality 1 in Fig.1: AB823111, AB823112, AB823113 [*cytb*]; AB823183, AB823184, AB823185 [*RAG1*];

China, Yunnan Province, Jingdong County, locality 10 in Fig.1: KC481348 [*cytb*]; KC481370 [*RAG1*]; KC481358 [*BRCA1*].

Euroscaptor sp.2:

Vietnam, Vinh Phuc Province, vicinity of Tam Dao, 21°27´06´´N, 105°38´09´´E, altitude 750m (Meegaskumbura et al. 2007; He et al. 2014), locality 2 in Fig.1: AB823108, AB823109, AB823110, EU122226 [*cytb*]; AB823180, AB823181, AB823182, JQ433897 [RAG1];

Vietnam, Cao Bang Province, Nguyen Binh (Shinohara et al. 2014), locality 13 in Fig.1: AB823114, AB823115, AB823116 [*cytb*]; AB823186, AB823187, AB823188 [*RAG1*].

Euroscaptor klossi:

Thailand, Chiang Rai, Mae Sa Long, 20°09´57.4´´N, 99°37´23.2´´E, elevation 1200m (Shinohara et al. 2014); locality 17 in Fig.1: AB823178, AB823179 [*cytb*]; AB823178, AB823179 [*RAG1*].

Euroscaptor malayana:

Malaysia, Pahang, Cameron Highlands, 4°27´N, 101°26´E, elevation of 1400m (Shinohara et al. 2014), locality 17 in Fig.1: AB185155, AB185156 [*cytb*]; AB185155, AB185156 [*RAG1*].

Euroscaptor subanura:

Vietnam, Ba Vi District, 50 km west of Hanoi, vicinity of Ba Vi Resort, 21°04´58´´N, 105°22´54´´E (our data), locality 5 in Fig.1: KP995370 [*cytb*]; KP995375 [*RAG1*]; KP995395 [*BRCA1*]; KP995388 [*BRCA2*]; KP995381 [*ApoB*]; KP995410 [*A2ab*].

Euroscaptor parvidens:

Vietnam, Quang Nam Province, Dong Giang District (He et al. 2014; Shinohara et al. 2014), locality 14 in Fig.1: AB823120, AB823121, AB823122 [*cytb*]; AB823192, AB823193, AB823194 [*RAG1*];

Vietnam, Dak Lak Province, Chu Yang Sin National Park, locality 15 in Fig.1. There is no exact locality information in published works (Kawada et al. 2009; Shinohara et al. 2014). We assume it can be Krong Bong District, Cu Pui Commune, based on locality data retrieved from Hughes (2010): AB823117, AB823118, AB823119 [*cytb*]; AB823189, AB823190, AB823191 [*RAG1*];

Vietnam, Kon Tum Province, Dac Glei District, 2-3 km west of Ngoc Linh Mt., 15°05´N, 107°57´E (Zemlemerova et al. 2013), locality 6 in Fig. 1: KC481342, KC481343, KC481344 [*cytb*]; KC481368 [*RAG1*]; KC481356 [*BRCA1*].

Vietnam, Lam Dong Province, Lac Duong District, 5 km NE Long Lanh Village, Bi Dup – Nui Ba Nature Reserve, 12°10´44´´N, 108°40´44´´E (Zemlemerova et al. 2013), locality 8 in Fig.1: KC481338, KC481339, KC481340, KC481341 [*cytb*]; KC481365, KC481366, KC481367 [*RAG1*]; KC481354, KC481355, [*BRCA1*]; KP717147 [*BRCA2*]; KP717257 [*ApoB*]; KP995408 [*A2ab*].

Euroscaptor mizura: AB037604, AB076828, AB823103, AB823104, AB823105, DQ630413 [*cytb*]; AB176543, AB823173, AB823174, AB823175, AB823176, AB823177 [*RAG1*]; HG737898, DQ630251 [*BRCA1*]; DQ630168 [*ApoB*].

Mogera robusta: KC481328 [*cytb*]; KC481361 [*RAG1*]; KC481351 [*BRCA1*]; KP717144 [*BRCA2*]; KP717255 [*ApoB*].

Mogera wogura: AB037646 [*cytb*]; HG737919 [*RAG1*]; HG737903 [*BRCA1*]; AB638557 [*A2ab*].

Mogera latouchei: KP717378 [*cytb*];

Talpa europaea: KF801564 [*cytb*]; KP717261 [*RAG1*]; KP717157 [*BRCA1*]; KP717098 [*BRCA2*]; KP717207 [*ApoB*].

Talpa occidentalis: KP717326 [*cytb*]; KP717272 [*RAG1*]; KP717161 [*BRCA1*]; KP717106 [*BRCA2*]; KP717219 [*ApoB*].

Talpa caucasica: KP717353 [*cytb*]; KP717298 [*RAG1*]; KP717187 [*BRCA1*]; KP717127 [*BRCA2*]; KP717240 [*ApoB*].

Talpa altaica: FN640579 [*cytb*]; KP717312 [*RAG1*]; KP717198 [*BRCA1*]; KP717139 [*BRCA2*]; KP717251 [*ApoB*].

Scaptochirus moschatus: HG737883, AB306502 [*cytb*]; HG737927, HG737927 [*RAG1*]; HG737911 [*BRCA1*].

Parascaptor leucura: HG737877, HG737878, HG737879, HG737880, HG737881, HG737882 [*cytb*]; HG737921, HG737922, HG737923, HG737924, HG737925, HG737926 [*RAG1*]; HG737905, HG737906, HG737907, HG737908, HG737909, HG737910 [*BRCA1*].

Desmana moschata: AB076836 [*cytb*]; KP717317 [*RAG1*]; KP717203 [*BRCA1*]; KP717148 [*BRCA2*].

Galemys pyrenaicus: AY833419 [*cytb*]; AY833415 [*RAG1*]; AY121757 [*BRCA1*]; AY121767 [*A2ab*].

Condylura cristata: AB076810 [*cytb*]; KP717319 [*RAG1*]; KP717205 [*BRCA1*]; KP717150 [*BRCA2*]; KP717260 [*ApoB*].

Parascalops breweri: KP717379 [*cytb*]; KP717318 [*RAG1*]; KP717204 [*BRCA1*]; KP717149 [*BRCA2*]; KP717259 [*ApoB*].

Appendix 2. List of the GenBank accession numbers from this study.

Species	Museum No.	GenBank accession no.					
		cytb	*RAG1*	*BRCA1*	*BRCA2*	*ApoB*	*A2ab*
Euroscaptor parvidens ngoclinhensis ssp. nov.	ZIN 96663	KC481342					
Euroscaptor parvidens ngoclinhensis ssp. nov.	ZIN 96664	KC481343					
Euroscaptor parvidens ngoclinhensis ssp. nov.	ZIN 96665	KC481344	KC481368	KC481356	KX164229	KX164193	KX164183
E. parvidens	ZIN 98916	KC481338	KC481365	KC481354	KX164228	KX164192	
E. parvidens	ZIN 98917	KC481339	KC481366	KC481355	KP717147	KP717257	KP995408
E. parvidens	ZIN 98918	KC481340	KC481367				
E. parvidens	ZIN 98919	KC481341					
E. parvidens	ZIN 101901	KX164254	KX164272	KX164214	KX164233	KX164196	
E. parvidens	ZIN 101902	KX164256	KX164274	KX164216	KX164234	KX164198	KX164186
E. parvidens	ZMMU S-195070	KX164255	KX164273	KX164215	KX164232	KX164197	
E. parvidens	ZMMU S-195071	KX164257	KX164275	KX164217	KX164235	KX164199	
E. parvidens	ZIN 101920	KX164249					
E. parvidens	ZIN 101921	KX164250	KX164270	KX164212	KX164230	KX164194	KX164184
E. parvidens	ZIN 101922	KX164251					
E. parvidens	ZIN 101923	KX164252	KX164271	KX164213	KX164231	KX164195	KX164185
E. parvidens	ZIN 102246	KX164248					
E. parvidens	ZIN 102247	KX164253					
E. subanura	ZIN 101533		KX164279	KX164221	KX164240	KX164204	
E. subanura	ZIN 101534	KX164261	KX164280	KX164222	KX164241	KX164205	KX164188
E. subanura	AVA 12-276	KX164260	KX164278	KX164220	KX164239	KX164203	
E. subanura	ZIN 101897	KX164262	KX164281	KX164223	KX164242	KX164206	
E. subanura	ZIN 101898	KX164263	KX164282		KX164243	KX164207	
E. subanura	ZIN 101899		KX164283	KX164224	KX164244	KX164208	KP995410
E. subanura	ZIN 101900	KP995370	KP995375	KP995395	KP995388	KP995381	
E. subanura	ZIN 101924	KX164264					
E. subanura	ZIN 101925	KX164265	KX164284	KX164225	KX164245	KX164209	KX164189
E. subanura	ZIN 101926	KX164266	KX164285	KX164226	KX164246	KX164210	KX164190
E. subanura	ZIN 101927	KX164268					
E. subanura	ZIN 102248	KX164267	KX164286	KX164227	KX164247	KX164211	KX164191
E. subanura	AVA 14-117	KX164269					
Euroscaptor orlovi sp. nov.	ZIN 96318	KC481345					KP995409
Euroscaptor orlovi sp. nov.	ZIN 97789	KC481347	KC481369	KC481357	KP717146	KP717258	
Euroscaptor orlovi sp. nov.	ZIN 98142	KC481346					
Euroscaptor orlovi sp. nov.	ZIN 99335	KC481348	KC481370	KC481358	KX164238	KX164202	
Euroscaptor kuznetsovi sp. nov.	ZIN 101531	KX164258	KX164276	KX164218	KX164236	KX164200	KX164187
Euroscaptor kuznetsovi sp. nov.	ZIN 101532	KX164259	KX164277	KX164219	KX164237	KX164201	

Appendix 3. Substitution models for the mitochondrial *cytb* gene and five nuclear genes employed in maximum likelihood analysis.

cytb	J2+G	HKY+G	GTR+G
ApoB	HKY+G		K80
BRCA1	TN+G		HKY+G
BRCA2	HKY		TVM
RAG1	F81+ G		K80+G
A2ab	K80+G		K81uf+G